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## Review

# Which MAT gene? Pezizomycotina (Ascomycota) mating-type gene nomenclature reconsidered

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### ABSTRACT

Filamentous fungi in the subdivision Pezizomycotina (Ascomycota) display an impressive diversity of mating strategies. These mating systems are all controlled by the mating-type (MAT) genes, some of which are conserved, even among distantly related genera. In order to facilitate effective communication between researchers, a system was established in 2000 to name these genes and this has subsequently been widely applied. However, due to the rapid growth in the number of described MAT genes in the Pezizomycotina, an evaluation of the manner in which the nomenclature system has been applied is warranted and revisions should be considered. We address this challenge by doing a systematic review of the nomenclature associated with the MAT1 locus and its associated genes described in the Pezizomycotina. Several problems in the application of the nomenclature system were identified and addressed. These included proposed revisions of the nomenclature system to provide a more accurate description of the mating-type genes. We anticipate that this review will reduce confusion and that it will be useful in future characterisation of mating-type genes.

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## 1. Introduction

In the early part of the 20th century, Albert Blakeslee initiated a study on members of the Mucorinae and inadvertently produced the first paper concerning sexual reproduction in the

fungi (Blakeslee, 1904). Although he focused on the morphology and physiology of the group, his discoveries on the behaviour of isolates during sexual reproduction have provided the cornerstone of subsequent studies on fungal mating systems. Later, the emergence of techniques such as cloning

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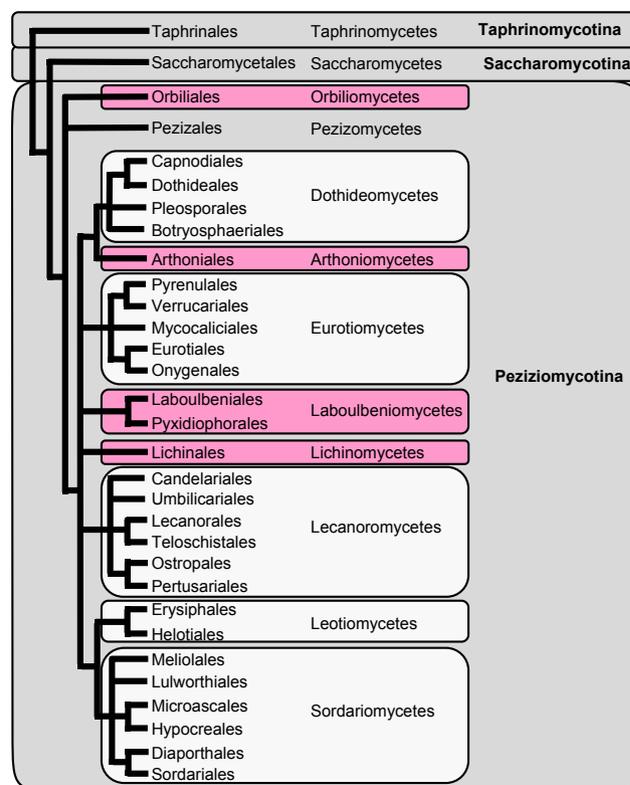
(Cohen et al., 1973; Jackson et al., 1972), PCR (Saiki et al., 1988) and Sanger sequencing (Sanger and Coulson, 1975; Sanger et al., 1977) provided the means to examine the molecular basis of sexual reproduction in a range of model fungi (e.g. Debuchy and Coppin, 1992; Glass et al., 1988; Kang et al., 1994; Picard et al., 1991). More recently, whole-genome sequencing technology has allowed for a shift of focus away from studying only model organisms (Davis, 2004; Muller and Grossniklaus, 2010), where a significant fraction of previous and current genome sequencing efforts are focused on fungi (Genomes OnLine Database; Grigoriev et al., 2011; Reddy et al., 2015). Not surprisingly, the availability of these data has allowed for the detailed characterization of the mating-type locus from many non-model fungi (e.g. Comeau et al., 2015; DiGuistini et al., 2011).

The naming of mating-type genes relies on a nomenclature system developed by Turgeon and Yoder more than 15 y ago (Turgeon and Yoder, 2000). The system applies names based on shared homology, allowing a single name to be used consistently, even across diverse fungal taxa. Where a novel mating-type gene has no known homology to any gene previously described from a fungal mating-type locus, a new name is assigned following a suite of guidelines. Although very elegant, the application of these rules has in some cases proved difficult, often resulting in inconsistent and ambiguous assignment of gene names. Such discrepancies represent significant barriers to meaningful discussions on the origin, functioning and evolutionary history of the genes underlying sexual reproduction in fungi (Debuchy et al., 2010; Debuchy and Turgeon, 2006; Dyer et al., 2016).

In this commentary, we provide an update of the nomenclatural system used for naming the mating-type genes of filamentous Ascomycetes in the subphylum Pezizomycotina (Fig. 1). To achieve this, we first review knowledge regarding gene content and organisation of the locus underlying sexual reproduction in these fungi. The known mating-type genes are then discussed and the problems associated with naming new (and sometimes known) mating-type genes are outlined. To provide a starting point for characterising the mating-type region in the Pezizomycotina, we end with an overview of the most common strategies that are used to identify the mating-type locus and its genes. We hope that this commentary and review will not only provide clarity on the names currently used for mating-type genes, but more importantly, that it will also be useful to avoid the pitfalls associated with naming these genes in future.

## 2. Position and architecture of the Pezizomycotina MAT1 locus

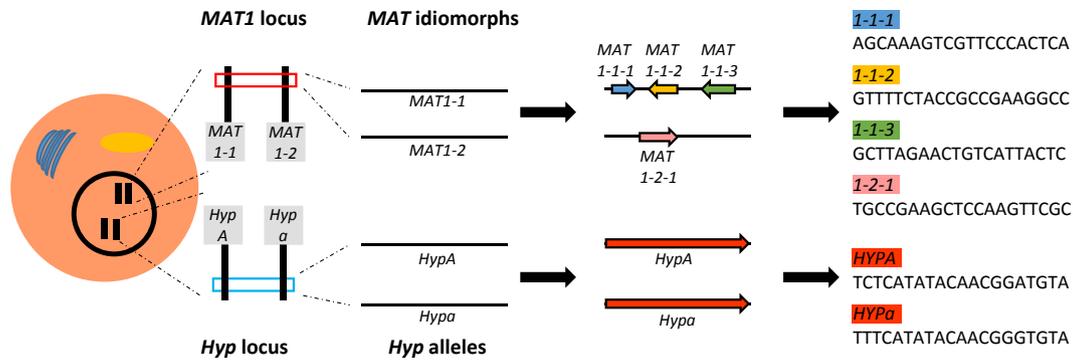
Despite utilizing diverse reproductive strategies (Billiard et al., 2011, 2012), almost all described Pezizomycotina have a bipolar mating system where sexual reproduction is controlled by a single genetic locus (Debuchy et al., 2010; Giraud et al., 2008). The concept of a single mating-type locus was established in the authoritative review of Whitehouse (1949) and subsequently confirmed through sequence-based characterization of the mating-type locus of *Neurospora crassa* (Glass et al., 1990; Staben and Yanofsky, 1990). The locus was later formally



**Fig. 1** – A schematic phylogeny of the subphyla in the Ascomycota. Shown are the classes that make up the subphylum Pezizomycotina, as well as representative orders within each class. The classes shown in red have no known published mating-type gene sequences. Phylogeny after Hibbett et al. (2007).

defined as the single position in the genome responsible for controlling mating (Turgeon and Yoder, 2000; Yoder et al., 1986) and named the MAT1 locus (Fig. 2; Turgeon and Yoder, 2000). Here the numeral “1” is used to indicate that only a single MAT locus is present in most Pezizomycotina studied to date (Turgeon and Yoder, 2000), although it does not exclude the possibility of additional loci that might be identified and would then be named MAT2, MAT3, and so forth (Turgeon and Yoder, 2000).

In all but one of the cases described (Cisar and TeBeest, 1999), the MAT1 locus of all heterothallic Pezizomycotina species studied thus far have two “versions” (Debuchy et al., 2010). These “versions” co-locate with the mating factors that were initially identified in *N. crassa* and shown to be linked to a putative mating-type chromosome (Lindgren, 1936a). Later work showed that the mating factors actually represent large chromosomal sections conferring mating specificity (Bistis, 1998; Lindgren, 1936b). Also, the two “versions” of these chromosomal sections are markedly different as they are maintained through the suppression of recombination between them (Dyer et al., 2016) and the genes they encode are highly divergent (Butler, 2007; Debuchy et al., 2010). Because the “versions” of the MAT1 locus do not conform to what is generally expected for true alleles (i.e. orthologous but alternative forms of a gene/marker at a locus; Griffiths et al., 2010), the term



**Fig. 2** – A comparison of the mating-type locus (top) and a somatic locus (bottom). In a diploid cell (the fusion product of two haploid cells), both the MAT1 locus and somatic locus is present on conserved positions on the chromosomes. These positions will house alternate versions of the gene products in heterothallic species: two idiomorphs (MAT1-1 and MAT1-2) for the mating-type locus and two alleles (Hyp A and Hyp a) for the somatic locus. The two idiomorphs house dissimilar genes that are unrelated in sequence. In comparison, alleles of the Hyp gene show a high level of sequence similarity. Representative short 20 bp DNA sequences are shown for illustration.

“idiomorph” was coined to denote them (Metzenberg and Glass, 1990). Specifically, the MAT1 locus of heterothallic Pezizomycotina has two idiomorphs, MAT1-1 and MAT1-2 (Fig. 2).

Individuals of heterothallic fungi (i.e., those that require interaction between opposite mating partners for completing the sexual cycle) harbour either one (never both) of the MAT1 idiomorphs (Debuchy and Turgeon, 2006; Turgeon and Yoder, 2000). Alignment of the corresponding sequences of compatible mating partners (i.e. individuals carrying either the MAT1-1 or MAT1-2 idiomorph) typically display substantial similarity outside the locus (including the regions immediately flanking it) and an overall lack of sequence similarity in the idiomorphic regions themselves (Glass et al., 1990; McGuire et al., 2001; Turgeon, 1998). Within this region of dissimilarity, the MAT1-1 idiomorph generally encodes one to three genes, while the MAT1-2 idiomorph often encode a single gene (Butler, 2007; Dyer et al., 2016).

The genomes of homothallic species (i.e. those with individuals that are self-fertile and capable of completing the sexual cycle in solo) commonly contain mating-type genes associated with both MAT1-1 and MAT1-2 idiomorphs (Butler, 2007; Debuchy and Turgeon, 2006; Yun et al., 1999, 2000). Relative to heterothallic species, their MAT1 locus structures are usually more complex (Butler, 2007; Wilson et al., 2015b; Yun et al., 2000). In the simplest situation, the MAT1-1 and MAT1-2 genes may be located at a single and relatively conserved genomic position, thus representing the MAT1 locus (Butler, 2007; Debuchy and Turgeon, 2006; Yun et al., 1999, 2000). The genes of the two idiomorphs can occasionally also occur at different genomic positions (e.g. Galagan et al., 2005; Paoletti et al., 2007; Rydholm et al., 2007; Yun et al., 1999), although the overall positional conservation (i.e. position in relation to genes known to be linked to the mating-type locus) are often the same as more typical MAT1 loci (Galagan et al., 2005).

The mating-type genes of the homothallic species *Cochliobolus cymbopogonis*, *Neosartorya fischeri* and *Aspergillus nidulans* provide examples of an atypical mating-type locus architecture. In these species, the mating-type genes are split across

two genomic positions (Paoletti et al., 2007; Rydholm et al., 2007; Yun et al., 1999). Each of these loci are flanked either by copies of the same genes present in their heterothallic counterparts (Paoletti et al., 2007; Yun et al., 1999), or by pseudogene versions of the flanking genes (Rydholm et al., 2007). The unusual mating-type loci of these species provide a unique challenge to the nomenclature system, and with the advent of genome sequencing, it is reasonable to expect that additional fungal species with atypical mating-type locus architecture will be identified. In a study of the mating-type genes of *As. nidulans*, Paoletti and co-workers (2007) implemented a system of naming proposed by G. Turgeon where the two genomic positions are each recognised as a unique MAT locus. The locus where the MAT  $\alpha$ 1 domain gene MAT1-1-1 (see section Genes encoded on the MAT1-1 idiomorph) is present was named MAT1, while the high-mobility group (HMG)-box domain MAT1-2-1 gene (see section Genes encoded on the MAT1-2 idiomorph) typified the MAT2 locus. That approach provides an elegant solution to the question of multiple mating-type loci in a single genome. Once identified, the genes present at each locus would be named following the standard nomenclature rules used to assign names in heterothallic species, i.e. the MAT1-1-1 present at the MAT1 locus remains MAT1-1-1, while the MAT1-2-1 gene present at the MAT2 locus will be named MAT2-2-1. This system could also be extended on a case-by-case basis for any additional mating-type loci (MAT3, MAT4 and so forth) characterised in future.

Comparisons of the MAT1 locus across the Pezizomycotina has revealed a high level of positional conservation as it is usually located at similar chromosomal positions (Butler, 2007; Debuchy and Turgeon, 2006; Dyer et al., 2016; Turgeon and Yoder, 2000). The genes immediately flanking the MAT1-1 and MAT1-2 idiomorphs typically include SLA2 that encodes the cytoskeleton assembly control protein and APN2 that encodes AP endonuclease. Since its emergence, roughly 400 million years ago (Idnurm, 2011), the SLA2-MAT1-APN2 configuration has been interrupted in certain fungi. The SLA2 gene in most Dothideomycetes is unlinked from the MAT1 locus

(Conde-Ferrázquez et al., 2007; Waalwijk et al., 2002), and its position adjacent to the locus appears to have been replaced by a unique gene named ORF1 (Open Reading Frame 1; Turgeon and Debuchy, 2007). There are also reports of ORF1 being linked to the MAT1 locus of some Sordariomycetes and Eurotiomycetes (Debuchy and Turgeon, 2006), although this gene has not been extensively studied. In several Dermatophytes (Eurotiomycetes) the APN2 and SLA2 genes are linked to one side of the MAT1 locus (Lee et al., 2010), and a similar architecture is present in *Ceratocystis fimbriata* (Sordariomycetes; Wilken et al., 2014). In *Huntia* (Sordariomycetes), APN2 appears not to be linked to the MAT1 locus (Wilson et al., 2015a), and in *Coccidioides* (Eurotiomycetes) the APN2 gene lies within the locus (Mandel et al., 2007).

The APC5 and COX13 genes, encoding the Anaphase Promoting Complex and subunit VIa of cytochrome c oxidase, respectively, have also been associated with the MAT1 locus of several Pezizomycotina lineages. Both genes are present near the MAT1 locus of species in the Sordariomycetes, Leotiomycetes, Eurotiomycetes and some Dothideomycetes (Bihon et al., 2014; Butler, 2007; Debuchy et al., 2010; Debuchy and Turgeon, 2006; Fraser et al., 2007). Both COX13 and APC5 is commonly linked to the APN2 gene (e.g. in *N. crassa*, *Gibberella zeae*, *Magnaporthe grisea*, *Podospora anserina* and *As. nidulans*), with COX13 often positioned between APN2 and APC5 (Bihon et al., 2014; Debuchy and Turgeon, 2006; Li et al., 2010; Tsui et al., 2013).

### 3. Problems naming genes in the MAT1 locus

The standardized nomenclature for fungal mating-type genes defines a MAT1 gene as an open reading frame present within the confines of the MAT1-1 and MAT1-2 idiomorphs (Turgeon and Yoder, 2000). Following this system, genes are named to reflect both the locus and idiomorph at which they are present (Fig. 2). As an example, the name MAT1-2-3 refers to the third (MAT1-2-3) gene present at the second idiomorph (MAT1-2-3) of the MAT1 locus (MAT1-2-3). An extensive database of known mating-type gene sequences is currently available in the public domain. This makes it possible to use sequence homology to assign gene names without much additional knowledge regarding the position of the genes within genomes (Dyer et al., 2016). This is especially true for those genes that show a wide distribution among fungi (Turgeon and Yoder, 2000). But, despite being straightforward and intuitively obvious to apply, this naming system does not always allow for unambiguous and clear decisions regarding the names of mating-type genes.

The first problem associated with the naming of mating-type genes pertains to processes that drive their evolution, which significantly influence their gene sequences. Mating-type genes are known to be under strong diversifying selection (Civetta and Singh, 1998; Martin et al., 2011; Turgeon, 1998) resulting in homologs showing low levels of conservation among different genera (Arie et al., 1997; Cisar et al., 1994). This complicates the identification and correct naming of mating-type homologs, especially in groups where mating-type genes have not yet been studied extensively. Due to the widespread nature of this problem (i.e. the mating-type genes have been characterised in <4 % of known Pezizomycotina species), the recent literature commonly describes novel

MAT1 genes with no known homologs (e.g. Bihon et al., 2014; Martin et al., 2011; Wilson et al., 2015a).

Another problem confounding the accurate identification of MAT gene homologs pertains to the quality of the sequences present in public domain databases. Putative mating-type genes are frequently deposited in the GenBank nucleotide repository (Benson et al., 2013) without obvious linkage to published work. As a result, the rigorous evaluations that commonly accompany peer review have often not provided prior screening for accuracy of the work. Thus, if any homology to these proteins is later identified, the assigned name could be erroneously applied to MAT1 genes across multiple taxa, further perpetuating the problem. For example, identification of the MAT1-1-4 gene in *Sphaeropsis sapinea* (= *Diplodia pinea*) was based on sequence similarity to putative MAT1-1-4 gene sequences from *Trichophyton verrucosum* and *Anthroderma benhamiae* (Bihon et al., 2014), but there is no published work relating to this gene in the latter two species (see section [Genes encoded on the MAT1-1 idiomorph](#)).

The processes fundamental to the evolution and maintenance of mating-type loci can also influence how mating-type genes are named. For example, initial cycles of recombination followed by widespread suppression of recombination can lead to the inclusion of apparently “non-mating-type genes” (i.e. those not commonly present in the MAT1 locus) within the idiomorphic regions of the MAT1 locus and their subsequent maintenance within the borders of the region (Mandel et al., 2007). Examples of this problem can be found in some *Coccidioides* species where genes with no known function in mating (i.e. COX13 and APN2) have been captured into an expanded MAT1 locus (Mandel et al., 2007). Because of their position, these genes were described as mating-type genes (e.g. MAT1-1-5 and MAT1-2-5 for the COX13 gene occurring on the two idiomorphs), but having multiple names for a gene with a conserved function is both redundant and confusing.

Another issue central to naming mating-type genes is how model species of *Neurospora* and *Podospora* were treated in early studies. The mating-type genes in these species were identified and named (Supplementary table 1) before the current nomenclature system (Barratt and Perkins, 1965; Perkins et al., 1982; Picard et al., 1991) was proposed. Consequently, this did not follow the model proposed by Turgeon and Yoder (2000). Although these genes share homology with the mating-type genes in other species (Dyer et al., 2016), the use of the species-specific names make it difficult to recognize similarly named homologs. While these species-specific gene names highlight the role played by model species in shaping our understanding of many biological processes (such as the evolution of the mating-type locus), we propose that the MAT-specific names (i.e. MAT1-1-1, MAT1-1-2, etc.) should be used in conjunction with the species-specific designations in future studies. This will make it possible for those not familiar with the *Neurospora* and *Podospora* mating-type gene literature to recognise the homology implied by the MAT-specific gene names.

All of these problems associated with the nomenclature system for mating-type genes add additional and unnecessary layers of complexity to studies on the structure, evolution and functioning of the MAT1 locus of fungi. Indeed, our examination of DNA sequences and the associated literature revealed that these problems regarding the naming of mating-type

genes are widespread in the Pezizomycotina. We found that the 16 known mating-type genes encoded in the Pezizomycotina *MAT1* locus (*MAT1-1-1* to *MAT1-1-7* from the *MAT1-1* idiomorph and *MAT1-2-1* to *MAT1-2-9* from the *MAT1-2* idiomorph) are linked to at least 24 distinct genes that have been described from diverse fungi. Below we provide a systematic review for each of these genes. Where this is deemed appropriate, changes to the nomenclature system are proposed (Table 1).

#### 4. Updated nomenclature for the *MAT1* genes of Pezizomycotina

When identifying mating-type genes, it is important that the correct names are used to illustrate similarity to existing *MAT* genes; also, to allow for direct comparisons between homologs. Correctly assigning a mating-type gene name can be

notoriously difficult, especially for genes with no known conserved domain or for those that show limited distribution across the Pezizomycotina. A reliable indicator of homology is the identification of conserved domains within the predicted protein, as is the case for proteins such as *MAT1-1-1* and *MAT1-2-1* (Table 1). Alternatively, homology can also be assessed on the basis of amino acid sequence similarity to known *MAT* proteins, which generally show levels of around 50 % identity. Here, it is important to recognise that this level can vary greatly based on the taxonomic relatedness of the species, although some homology in at least parts of the protein can usually be identified. Another indicator of a putative homolog is the presence of the *MAT* gene under investigation in related taxonomic groups (Table 1). A new sequential *MAT* gene number should only be introduced where homology to known mating-type genes cannot be found. In the following section, we describe a series of known *MAT* genes that provide a guide to the identification of newly identified mating-type genes.

**Table 1 – The known mating genes of species belonging to the Pezizomycotina, with the alternative gene names suggested here printed in bold type. A dataset of representative proteins carrying the new names is available from <http://dx.doi.org/10.6084/m9.figshare.4625986>.**

MAT gene name		Pfam domain	Known distribution	Representative protein	
Original	Revised			Species	Accession
<b>MAT1-1</b>					
<i>MAT1-1-1</i>	<i>MAT1-1-1</i>	PF04769 – MAT $\alpha$ 1 HMG-box	All Pezizomycotina	<i>Neurospora crassa</i>	ESA43845 <sup>a</sup>
<i>MAT1-1-2</i>	<i>MAT1-1-2</i>	PF17043 – Unknown	Sordariomycetes	<i>N. crassa</i>	EAA35087 <sup>a</sup>
<i>MAT1-1-3</i>	<i>MAT1-1-3</i>	PF00505 – HMG box	Sordariomycetes and Leotiomyces	<i>N. crassa</i>	EAA35088 <sup>a</sup>
<i>MAT1-1-4</i>	<i>MAT1-1-4</i>	None	Leotiomyces	<i>Pyrenopeziza brassicae</i>	CAA06845
<i>MAT1-1-4</i>	<b><i>MAT1-1-8</i></b>	None	Dothideomycetes	<i>Sphaeropsis sapinea</i>	AHA91691
<i>MAT1-1-4</i>	<b><i>MAT1-1-9</i></b>	None	Eurotiomycetes	<i>Trichophyton verrucosum</i>	XP003023854
<i>MAT1-1-5</i>	<i>MAT1-1-5</i>	None	Leotiomyces: Helotiales	<i>Botrytis cinerea</i>	AHX22633
<i>MAT1-1-5<sup>b</sup></i>	COX13	PF02046 – COX6A	Eurotiomycetes: Coccidioides species	<i>Coccidioides immitis</i>	ABS19615
<i>MAT1-1-6</i>	<i>MAT1-1-6</i>	None	Leotiomyces: Pseudoeurotiaceae	<i>Pseudogymnoascus destructans</i>	AIG95729
<i>MAT1-1-6<sup>c</sup></i>	APN2	PF03372 – Exo-endo phos	Eurotiomycetes: Coccidioides species	<i>Co. immitis</i>	ABS19616
<i>MAT1-1-7<sup>d</sup></i>	<i>MAT1-1-7</i>	None	Eurotiomycetes	<i>Co. immitis</i>	ABS19617
<b>MAT1-2</b>					
<i>MAT1-2-1</i>	<i>MAT1-2-1</i>	PF00505 – HMG box	All Pezizomycotina	<i>N. crassa</i>	AAA33598 <sup>a</sup>
<i>MAT1-2-2</i>	<i>MAT1-2-2<sup>e</sup></i>	None	Sordariomycetes: <i>N. crassa</i>	<i>N. crassa</i>	– <sup>e</sup>
<i>MAT1-2-2</i>	<b><i>MAT1-2-6</i></b>	PF00505 – HMG box	Sordariomycetes: <i>Magnaporthe grisea</i>	<i>M. grisea</i>	BAE66607
<i>MAT1-2-3</i>	<i>MAT1-2-3</i>	PF11051 – Mannosyl trans3	Eurotiomycetes: Coccidioides species	<i>Co. immitis</i>	KMP00264
<i>MAT1-2-3</i>	<b><i>MAT1-2-9</i></b>	None	Sordariomycetes: Hypocreales	<i>Fusarium fujikuroi</i>	AEP03799
<i>MAT1-2-4</i>	<i>MAT1-2-4</i>	None	Eurotiomycetes	<i>Co. immitis</i>	XP001246636
<i>MAT1-2-4</i>	<b><i>MAT1-2-10</i></b>	None	Leotiomyces	<i>B. cinerea</i>	CDF43998
<i>MAT1-2-5</i>	COX13	PF02046 – COX6A	Eurotiomycetes: Coccidioides species	<i>Coccidioides immitis</i>	XP001246633
<i>MAT1-2-5<sup>f</sup></i>	<b><i>MAT1-2-5<sup>f</sup></i></b>	None	Dothideomycetes: <i>Sp. sapinea</i>	<i>Sp. sapinea</i>	AHA91682
<i>MAT1-2-5</i>	<b><i>MAT1-2-11</i></b>	None	Leotiomyces: <i>Pseudogymnoascus</i> species	<i>Ps. destructans</i>	AIG95713
<i>MAT1-2-6</i>	APN2	PF03372 – Exo-endo phos	Eurotiomycetes: Coccidioides species	<i>Co. immitis</i>	XP001246634
<i>MAT1-2-7</i>	<i>MAT1-2-7</i>	None	Sordariomycetes: <i>Huntia</i> and <i>Knoxdaviesia</i> species	<i>H. omanensis</i>	AOY41711
<i>MAT1-2-8</i>	<i>MAT1-2-8</i>	None	Sordariomycetes: Hypocreales	<i>Villosiclava virens</i>	AKE48512

a The naming of the mating-type genes for *Neurospora crassa* predates the establishment of the current nomenclature system, and as such differs from the standard notation. See section [Problems naming genes in the \*MAT1\* locus](#) for more information.

b The sequence was described as *MAT1-1-5* (Mandel et al., 2007), but was deposited as *MAT1-1-2*.

c The sequence was described as *MAT1-1-6* (Mandel et al., 2007), but was deposited as *MAT1-1-3*.

d The sequence was described as *MAT1-1-7* (Mandel et al., 2007), but was deposited as *MAT1-1-4*.

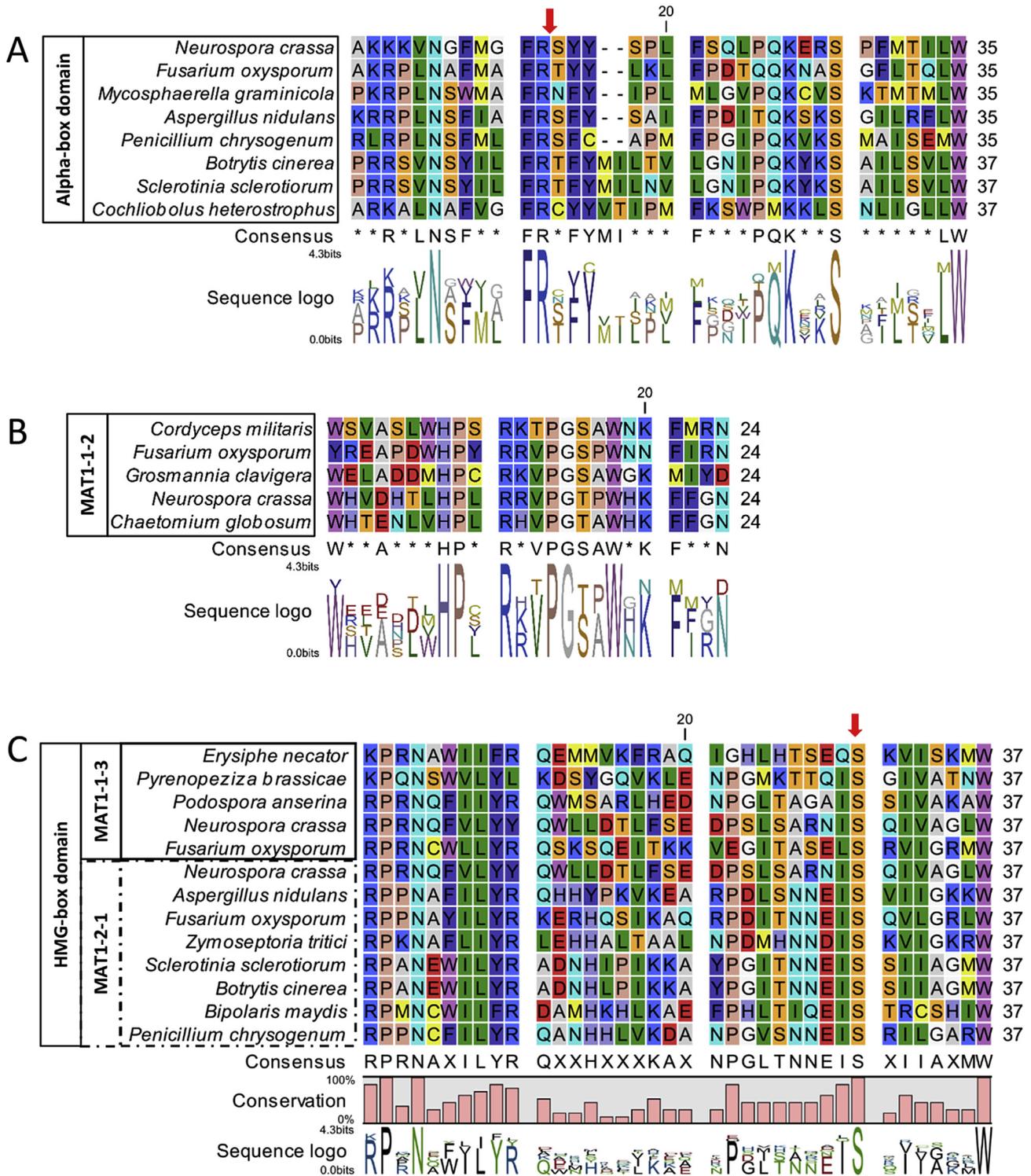
e While the *MAT1-2-2* gene in *N. crassa* was predicted (Klix et al., 2010; Pöggeler and Kück, 2000), the corresponding protein was never annotated in the Genbank database. See section [Genes encoded on the \*MAT1-2\* idiomorph](#) and [Supplementary Fig. 1](#) for detail.

f The name *MAT1-2-5* was suggested by Bihon et al. (2014), but was changed to *MAT1-2-9* in a later study (Wang et al., 2016). We propose that the *MAT1-2-5* name be retained (see section [Genes encoded on the \*MAT1-2\* idiomorph](#) for details).

## Genes encoded on the MAT1-1 idiomorph

The MAT1-1-1 gene (Fig. 3) characterises the MAT1-1 idiomorph (Debuchy et al., 2010; Turgeon and Yoder, 2000), and

as such has been the focus of a number of thorough reviews (Debuchy et al., 2010; Debuchy and Turgeon, 2006; Dyer et al., 2016; Martin et al., 2010). First described from the *matA* (= MAT1-1) idiomorph of *N. crassa* (Glass et al., 1990;



**Fig. 3** – An alignment of part of the (A) MAT1-1-1 alpha-box, (B) MAT1-1-2 conserved domain and (C) HMG-box domain of the MAT1-1-3 (solid block) and MAT1-2-1 (dashed block) proteins. The consensus sequences are based on a 60 % similarity cut-off, while the sequence logo illustrates the relative representation of each amino acid per position. Red arrows indicate the position of conserved introns. Figure produced using GLC Main Workbench v7.6.4; details of the sequences are available in the supplementary info (Supplementary table 2).

Metzenberg and Glass, 1990), the MAT1-1-1 gene encodes a DNA-binding protein with a conserved MAT $\alpha$ 1 domain (Arnaise et al., 1993; Debuchy et al., 2010), an identifying characteristic of this protein (Table 1). This motif is ancestrally related to the HMG-box domain class, MATA\_HMG (Martin et al., 2010; Soullier et al., 1999), which forms part of a group of motifs shared between fungal mating-type genes, T-cell transcription factors (TCF), and the Sex-determining Region of the Y-Chromosome (Sry) in animals (Soullier et al., 1999). Some authors also consider an intron present in a conserved position within the MAT $\alpha$ 1 domain (Fig. 3) as characteristic of the MAT1-1-1 gene (Kanematsu et al., 2007; Waalwijk et al., 2002; Wilken et al., 2014), although this intron might not be universally present (e.g. the human pathogen *Sporothrix schenckii*; Teixeira et al., 2015).

The MAT1-1-2 gene was the second MAT1-1 gene to be described (Turgeon and Yoder, 2000) and is known only in members of the Sordariomycetes (Debuchy et al., 2010; Debuchy and Turgeon, 2006). Several studies have attempted to define a reliable conserved domain for this protein (Debuchy and Turgeon, 2006; Kanematsu et al., 2007), and such a motif is now included in the Protein Family (PFAM) database (Fig. 3; Dyer et al., 2016). Deletion analysis has shown that this gene plays a role in ascocarp formation (Arnaise et al., 2001; Klix et al., 2010; Zheng et al., 2013), although the exact function of MAT1-1-2 in sexual reproduction remains unresolved.

The MAT1-1-3 gene carries an HMG-box domain (Fig. 3) from the MATA\_HMG-box class (Soullier et al., 1999). MAT1-1-3 is known only from the MAT1-1 idiomorph of the Sordariomycetes and Leotiomyces (Debuchy et al., 2010). Although MAT1-2-1 also carries this HMG-domain (see section Genes encoded on the MAT1-2 idiomorph), it is quite distinct from that of MAT1-1-3 (Debuchy et al., 2010; Debuchy and Turgeon, 2006; Jacobi et al., 2010). Different from the MAT1-2-1 gene, MAT1-1-3 also lacks the conserved C-terminal PRkXseXrrR sequence (Debuchy et al., 2010). The open reading frames for both MAT1-2-1 and MAT1-1-3 include an intron located across the first nucleotide of the codon that codes for a serine residue within the HMG-domain (Fig. 3; Arie et al., 1997, 2000; Debuchy and Turgeon, 2006).

MAT1-1-4 was first described from the MAT1 locus of the heterothallic *Pyrenopeziza brassicae* (Leotiomyces) as a novel mating-type gene with homology to known metallothionein proteins (Singh and Ashby, 1998). A putative homolog of this gene was subsequently detected in *Tapesia yallundae*, a species belonging to the same family as *Py. brassicae* (Singh et al., 1999), leading to suggestions that MAT1-1-4 might be associated with the mating-type region of all Leotiomyces (Debuchy et al., 2010). Apart from MAT1-1-4, no other fungal mating-type proteins harbouring a metallothionein domain have been described, making it difficult to assign a possible function for this gene. Metallothionein proteins have been strongly implicated in the regulation of cellular growth and differentiation through maintaining homeostatic control of heavy metal levels (Thirumoorthy et al., 2007). Based on this fact, it has been proposed that the expression of MAT1-1-4 might be initiated by senescence of the host leaf that leads to the accumulation of heavy metal ions (Singh et al., 1999). This could be important in species such as *Py. brassicae*

and *Ta. yallundae* that both produce sexual structures on senescing plant tissue (Dyer et al., 1994; McCartney and Lacey, 1990).

A second MAT1-1-4 gene has been described from *Sp. sapinea* (Bihon et al., 2014). These authors reported the gene name based on limited amino acid homology to putative and unpublished MAT1-1-4 proteins of the Eurotiomycetes *Tr. verrucosum* and *An. benhamiae*. However, this similarity (12–18 %) falls well below the levels typically encountered among homologous MAT1 genes (usually > 50 % amino acid identity, although it can vary based on relatedness of the species). This was true for the comparisons between *Sp. sapinea* and *Py. brassicae*, as well as comparisons with the two Eurotiomycetes. Based on these data, and considering the lack of additional functional information for these genes, we propose that the gene in *Sp. sapinea* is renamed MAT1-1-8 while the gene present in the Eurotiomycetes is renamed MAT1-1-9 (Table 1). This would be consistent with the broad acceptance of the metallothionein encoding MAT1-1-4 gene name across multiple publications related to mating (Foster and Fitt, 2003; Groenewald et al., 2006; Pöggeler, 2001; Turgeon and Yoder, 2000; Zaffarano et al., 2010). By following this relatively conservative approach to naming, these three genes and their products will likely each be afforded scientific scrutiny, which should ultimately reveal their role(s) in the biology of the fungi harbouring them.

The MAT1-1-5 and MAT1-1-6 genes were originally applied to idiomorph-specific versions of the respective COX13 and APN2 genes from several *Coccidioides* species (Mandel et al., 2007). Versions of these genes were also identified in the MAT1-2 idiomorph and were named MAT1-2-5 and MAT1-2-6. The two idiomorph-specific COX13 and APN2 proteins were significantly diverged, showing only 76.4 % and 53.7 % amino acid identity, respectively. These genes are expressed under all developmental conditions and appear to be the only copies of each gene in the genome (Mandel et al., 2007). This points to the fact that both COX13 and APN2 were captured into an expanding mating-type locus, rather than being true mating-type genes. As mentioned previously, the assignment of a MAT gene name to proteins with functions other than in mating, complicates the study of the MAT1 locus. We, therefore, propose that these genes should not be referred to as MAT genes, but rather be known as idiomorph-specific versions of COX13 and APN2.

The names MAT1-1-5 and MAT1-1-6 have also been used to describe novel mating-type genes in certain Leotiomyces (Table 1). MAT1-1-5 was described from the MAT1-1 idiomorph of *Botrytis cinerea* (Amselem et al., 2011), *B. elliptica* (Bin Terhem et al., 2015), *Sclerotinia sclerotiorum* (Amselem et al., 2011; Chitrampalam et al., 2013) and *Rutstroemia sydowiana* (Van der Nest et al., 2014). The name MAT1-1-6 was assigned to a gene present in three species of *Pseudogymnoascus*, which includes *Ps. destructans* that causes white-nose syndrome of bats (Palmer et al., 2014). The role of MAT1-1-5 and MAT1-1-6 and their products in the biology of these fungi has not yet been determined.

Only a single MAT1-1-7 gene has been named for a predicted protein of unknown function present in the MAT1-1 idiomorph of several *Coccidioides* species (Mandel et al., 2007). This gene has been reported to be present in the genomes of

additional members of the Eurotiomycetes, but appears to be absent from *Aspergillus* species (Mandel et al., 2007).

### Genes encoded on the MAT1-2 idiomorph

MAT1-2-1 is the archetypal MAT1-2 gene and it defines this idiomorph in all studied Pezizomycotina. The protein encoded by this gene harbours a MATA\_HMG-box class domain (Fig. 3) that has been shown to function in DNA binding across the plants, animals, and fungi (Ait Benkhali et al., 2013; Grosschedl et al., 1994; Laudet et al., 1993). As mentioned earlier, this gene is quite distinct from the HMG-box-harboursing MAT1-1-3 gene (Ait Benkhali et al., 2013; Debuchy et al., 2010; Debuchy and Turgeon, 2006; Jacobi et al., 2010), and contains the expected PRkXseXrrR sequence in its conserved C-terminal. However, the open reading frame for MAT1-2-1 includes an intron located at the same position as MAT1-1-3 (Fig. 3; Arie et al., 1997; Debuchy and Turgeon, 2006).

A MAT1-2-2 gene (initially described as mat a-2) was proposed in the MAT1-2 idiomorph of the model fungus *N. crassa* (Klix et al., 2010; Pöggeler and Kück, 2000). No GenBank accession number for the protein was included, although the published annotation for the gene was based on a previously deposited nucleotide sequence. Also, no function was assigned for this MAT1-2-2 gene (Klix et al., 2010). We were not able to identify this gene due to a discrepancy between the nucleotide sequence published and the sequence present in GenBank (Supplementary Fig. 1). Nevertheless, we propose that the MAT1-2-2 name remains reserved for this gene, although additional work is required to confirm its validity.

The name MAT1-2-2 has been used to designate a second HMG-box domain protein at the MAT1-2 idiomorph of *M. oryzae* (Sordariomycetes) (Kanamori et al., 2007). Although only the initiator methionine forms part of the idiomorph, this gene is expressed in a mating-specific manner. The presence of an HMG-box domain in MAT1-2-2 could point to a possible function as a DNA-binding protein, but no role for this gene in the mating process has been established (Kanamori et al., 2007). To avoid confusion between the *N. crassa* and *M. oryzae* MAT1-2-2 genes, we propose that the *M. oryzae* gene is renamed to MAT1-2-6 (Table 1).

The first description of a MAT1-2-3 gene originated from the MAT1-2 idiomorph of several *Coccidioides* species (Table 1; Mandel et al., 2007). This gene was reported to encode a novel protein with a mannosyl transferase-like function. Although the gene was not present in the other Eurotiomycetes examined (Mandel et al., 2007), it is present and expressed at only the MAT1-2 idiomorph of *Coccidioides*. An additional MAT1-2-3 gene, unrelated to that of *Coccidioides* was identified from the MAT1 locus in various Sordariomycetes, including several *Fusarium* species, *Cordyceps militaris* and *Paecilomyces tenuipes* (Martin et al., 2011), as well as *Clonostachys rosea* (Karlsson et al., 2015). Therefore, to avoid confusion we propose that the homolog found in *Coccidioides* retain the MAT1-2-3 name, while the one occurring in the Sordariomycetes be renamed MAT1-2-9.

The first description of the MAT1-2-4 gene emerges from research on the MAT1 locus of *Coccidioides* species (Mandel et al., 2007). Homologs have been reported in various Eurotiomycetes, including *As. fumigatus*, *As. fischeri*, *Histoplasma*

*capsulatum* and *Penicillium marneffeii* (Bubnick and Smulian, 2007; Mandel et al., 2007; Paoletti et al., 2005; Rydholm et al., 2007; Woo et al., 2006). An unrelated gene with the same name has also been reported in *B. cinerea* (Amselem et al., 2011), with homologs occurring in other Leotiomycetes (i.e. *Sc. sclerotiorum*, *Sc. trifoliorum* and *Ru. sydowiana*; Amselem et al., 2011; Van der Nest et al., 2014; Xu et al., 2016). Although the functions of these two genes remain to be investigated, we propose that the name of the gene in the Eurotiomycetes is retained, while the Leotiomycetes gene is renamed MAT1-2-10 (Table 1).

Similar to the case for MAT1-1-5 and MAT1-1-6, the names MAT1-2-5 and MAT1-2-6 were originally applied to idiomorph-specific versions of the respective COX13 and APN2 genes from several *Coccidioides* species (Mandel et al., 2007). As for the former two genes, we also propose that these genes are not referred to as mating-type genes, but rather idiomorph-specific versions of COX13 and APN2. However, the MAT1-2-5 name has also been applied to two unrelated genes, both of which harbour conserved domains for which structure-based functions could not be inferred. One of the genes was reported from *Sp. sapinea* (Bihon et al., 2014) as MAT1-2-5, with a homolog later identified in another Dothideomycetes species *Phyllosticta citricarpa* (Wang et al., 2016). The authors of the latter study recognized that the MAT1-2-5 gene name is invalid due to its use in *Coccidioides*, and changed the name to MAT1-2-9. We propose that MAT1-2-5 be retained for both the *Sp. sapinea* and *Ph. citricarpa* homologs as we believe that this gene name is invalid in *Coccidioides* (see above). Another MAT1-2-5 gene, unrelated to that of *Sp. sapinea* and *Ph. citricarpa*, was described from *Ps. destructans* (Palmer et al., 2014), and to avoid confusion should be renamed MAT1-2-11 (Table 1).

MAT1-2-7 is known only in a limited number of Sordariomycetes. The encoded MAT1-2-7 protein lacks detectable conserved domains and is exclusively present at the MAT1 locus of two *Huntia* and two *Knoxdaviesia* species (Aylward et al., 2016; Wilson et al., 2015a). The MAT1-2-8 gene has been described from the MAT1-2 idiomorph of the causal agent of rice false smut, *Villosiclava virens* (Yu et al., 2015). Expression of this gene was detected during both vegetative and sexual growth, and as such does not appear to play a direct role in mating. A homolog of MAT1-2-8 has been reported from *Metarhizium*, *Trichoderma*, *Ophiocordyceps*, *Torrubiella* and *Stachybotrys* (Yu et al., 2015), suggesting that it might be restricted to the Hypocreales.

## 5. Characterizing the MAT1 locus and its genes

Identification and sequence analysis of the MAT1 locus represent the first and fundamental step in studying the reproductive strategy of fungal species. Initially this was accomplished using mainly molecular biology approaches. For example, the *N. crassa* MAT1 genes were initially isolated using cloning techniques (Glass et al., 1988) and then used as probes to identify the MAT1 genes of *Po. anserina* (Picard et al., 1991). These early studies laid the foundation for subsequent research employing degenerate PCR (Arie et al., 1997; Barve et al., 2003; Conde-Ferráz et al., 2007; Singh et al., 1999; Witthuhn et al.,

2000) combined with genome and gene-walking approaches (Arzanlou *et al.*, 2010; Coelho *et al.*, 2008; McGuire *et al.*, 2001) to identify the mating-type genes in a relatively large number of fungal species. More recently, whole genome sequencing combined with BLAST (Basic Local Alignment Search Tool; Altschul *et al.*, 1990) has become widely used for the *in silico* identification of MAT1 genes (Dyer *et al.*, 2003; Li *et al.*, 2013; Martinez *et al.*, 2004; Pöggeler, 2002; Wilken *et al.*, 2014; Wilson *et al.*, 2015a). This wealth of existing information thus represents an invaluable resource to characterize the MAT1 locus in fungi.

The relatively conserved genomic location of the MAT1 locus (Butler, 2007; Debuchy and Turgeon, 2006; Dyer *et al.*, 2016) allows for its characterization using synteny-based approaches. Rather than searching for MAT1 genes where the sequences may show significant levels of divergence, even among closely related taxa (Arie *et al.*, 1997; Cisar *et al.*, 1994), the locus can be identified by locating the conserved genes that flank it (Turgeon, 1998). For example, the co-occurrence of ORF1 and the MAT1 locus has been useful for amplifying and cloning the mating-type region in a number of Dothideomycetes (Bennett *et al.*, 2003; Inderbitzin *et al.*, 2006; Turgeon, 1998; Vaghefi *et al.*, 2014; Yun *et al.*, 1999).

In the modern molecular genetics era, most studies seeking to characterize the MAT1 locus of Pezizomycotina will likely have access to whole genome data. The ease with which the MAT1 locus can be identified using these data will depend on various issues pertaining to the quality and completeness of the genome data and the availability of external evidence (e.g. expression of genes, thallism, mating strategies, etc.). However, application of the existing knowledge of the positional conservation and architecture of the MAT1 locus should provide reliable fundamental knowledge regarding its basic structure. Below, we suggest a basic approach that could be modified on a case-by-case basis to effectively characterise MAT1.

### A practical approach to characterising the MAT1 locus

Following genome assembly, a BLAST search (Altschul *et al.*, 1990) against the genome can be used to identify genomic regions containing mating-type genes. This could be based on a BLASTn, tBLASTx or BLASTp approach using the conserved MAT1-1-1, MAT1-1-2, MAT1-1-3 and/or MAT1-2-1 genes or proteins as a query. Although this is often sufficient to identify the MAT1 locus, a BLAST search with the genes (e.g. SLA2, APN2, APC or COX13) known to flank the locus would allow for a more detailed delimitation of the locus. Further laboratory-based work might be needed to obtain the complete sequence of the MAT1 locus and/or its individual genes. This is because the MAT1 locus often includes repetitive sequences that preclude its complete assembly from high-throughput sequence data. For example, the MAT1 locus of *Ce. fimbriata* was partly assembled from full genome sequences, but the presence of 260 bp direct repeats necessitated additional experimental work to obtain the full locus sequence (Wilken *et al.*, 2014). Similarly, the MAT1 locus of *Sc. trifoliorum* was partially assembled from genome sequencing, but was completed using conventional sequencing techniques (Xu *et al.*, 2016).

Prediction of the genes encoded at the MAT1 locus can then be achieved using *ab initio* prediction tools such as AUGUSTUS (Stanke *et al.*, 2006) and FGENESH (Solovyev *et al.*, 2006). These predictions can then be improved using evidence-based annotation software that takes into account homology with known proteins and expression (Yandell and Ence, 2012). The latter is particularly important for MAT1 genes where the accuracy of gene models often depends on the availability of RNAseq or Expressed Sequence Tag (EST) data. Alignment of the predicted proteins to known MAT1 genes can also allow for the optimization of gene models, although this is not feasible for the identification of novel mating-type genes. Computer software that can utilize such external evidences for the optimization and annotation of gene models include GeneWise (Birney *et al.*, 2004), GrailEXP (Hyatt *et al.*, 2000) or MAKER (Cantarel *et al.*, 2008).

Once gene models are available, their accuracy and annotations should be curated manually. This can be done using the information provided in Table 1, which summarizes the inferred protein families (if any) and distribution of the known MAT1 genes and lists the accession numbers for suitable representative sequences. The final gene models, together with appropriate references, should then be deposited in a public domain database to allow future comparisons with other work.

## 6. Future prospects

The genomics “revolution” has provided unprecedented access to the mating-type locus in fungi, resulting in mating-type genes being identified with minimum effort (Amselem *et al.*, 2011; Galagan *et al.*, 2005; Wilken *et al.*, 2014). This is a trend that is set to continue and grow and will surely provide invaluable resources to address questions regarding the evolution of the mating-type locus and associated genes. The availability of mating-type gene information from a wide range of species will also allow for a broader view on the evolution of sexual reproduction in the fungi. All of these studies require a robust and reliable nomenclature system for the mating-type genes. In this commentary and review, we have attempted to propose a system that could be useful to those describing mating-type genes.

An important future challenge lies in assigning biological functions to the large number of newly identified mating-type genes. Although there is value in knowing the distribution of mating-type gene homologs across different fungal lineages, this does not necessarily imply an understanding of their functions. The naming of mating-type genes relies on the accurate assignment of homology to distantly related genes, a process that will be informed by the knowledge of shared function. The development of improved genetic tools (Nødvig *et al.*, 2015) could provide the impetus needed to close the ever-widening gap between MAT gene descriptions and assignment of a biological function to them.

## Conflict of interest

None declared.

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## Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.fbr.2017.05.003>.

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